

The University of Chicago

STUDIES IN MASS PHYSIOLOGY: THE
EFFECT OF NUMBERS UPON THE
OXYGEN CONSUMPTION OF FISHES

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

1932

By
FRANK SCHUETT

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STUDIES IN MASS PHYSIOLOGY: THE EFFECT OF NUMBERS UPON THE OXYGEN CONSUMPTION OF FISHES¹

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INTRODUCTION

The study of animal aggregations during the past few years in this and other laboratories has uncovered a large group of interesting and valuable facts concerning the reactions and relations of animals when placed with others of their kind. This body of data has recently been reviewed by Allee ('31). Evidences of a "group effect" have been based upon such things as growth, reproductive rates, survival under toxic conditions, and other similar indices. In the fishes there has been some work on the effects and causes of aggregations. Church ('27) has shown that the growth of certain tropical fishes is conditioned to a considerable extent by the number of individuals present in the aquaria. The retardation of growth when larger numbers were present was ascribed to the presence of accumulated excretory products. Other workers have come to the same conclusions concerning the effects on growth produced by crowding of fishes (Willer and Schnigenberg, '27; Kawajiri, '28).

Much of the work on fish aggregations has dealt with species which ordinarily form schools in nature. Such aggregations seem distinctly different from the vast majority of fishes which do not appear to have the "schooling instinct." An interesting problem presents itself in bridging the gap between the solitary forms and those which exhibit highly integrated mechanisms of aggregation. It was thought probable that even in fishes which show no schooling reactions but which tolerate the nearby presence of other fishes there may be some measurable physiological effect of grouping or crowding other than the effects of growth, knowledge of which would open the way to further investigations upon the general problem of aggregations. Such effects have already been reported. Welty ('30) has shown that in goldfishes, which have not been considered as social, there are differences in learning behavior according to whether the fishes are single or in groups. Thus, it may be that even in animals which have hitherto been thought of as non-schooling, or non-social, there are influences producing effects which have so far been either overlooked or neglected.

¹ The writer wishes to express his appreciation to Professor W. C. Allee of the University of Chicago for the many helpful suggestions given during the course of this work.

It is the purpose of this paper to examine the respiratory behavior of certain fishes which exhibit little or no schooling tendency in order to determine to what extent a "group effect" is present.

MATERIALS AND METHODS

For this work four genera of fishes were employed. The guppy, *Lebistes reticulatus* Peters, the common mudminnow, *Umbra limi* Kirtland, the goldfish, *Carassius auratus* Linne, and the Atlantic killifish, *Fundulus heteroclitus* Linne served as test animals, and essentially similar results have been obtained in each case. The work was started with the mudminnows, but because of the unavailability of these in certain parts of the year it was necessary to resort to the others.

The oxygen consumption was determined by the Winkler method, Birge and Juday's modification ('11) being used in all cases. Objections to this method, especially as applied to studies of this sort (Heilbrunn, '15) center about the fact that a certain amount of free iodine is removed from the samples by fixation or adsorption because of the presence of slime or of excretory products of the test animals. The seriousness of this defect in the method was tested in the following manner:² Four fishes were placed in an open Erlenmeyer flask in one liter of water and left for thirty hours. Samples were taken from this water and iodine of a known strength added. Titrations were made with sodium thiosulfate and the available iodine recovered. The results thus obtained were checked with similar experiments on pure water under identical circumstances. It was found that in the thirty hours enough material was produced by the four fishes to remove the equivalent of 0.00209 cc. of oxygen from the samples. This period of thirty hours is over three times as long as any of the experimental periods, and hence the amount of slime will be in excess of that produced in the experiments. In the running water experiments to be described later the amount of iodine removed by adsorption is even smaller. Since only a negligible amount of iodine is adsorbed in thirty hours, and as the experiments were of a much shorter duration, the amount of removed iodine cannot be regarded as of significance.

Three different methods of experimentation were used which yielded essentially similar results. In all cases Whitman Laboratory well water was used. This was collected in a large carboy and aerated with air for some time before use. It was transferred from the carboy directly to the respiratory chambers. In the case of the running water experiments to be described later, a constant stream of this water was supplied to the respiratory chambers during the course of the experiment. The methods used were as follows:

1. Determination of the oxygen concentration in the medium before and after an experiment with the container stoppered to avoid air contamination during the time of experimentation. This method has been criticised, espe-

² The cooperation of Mr. R. B. Oesting in these chemical analyses is gratefully acknowledged.

cially when the period of time over which the experiment is run is rather long, because of the complications involved when carbon dioxide and other products of metabolism collect in the medium in which the test animals are living, and also because of the reduction of available oxygen as time goes on. In the present work one and two hour intervals were used, but even here there is the possibility of contamination with excretory products having influenced the oxygen consumption.

2. Determination of the oxygen concentration at intervals during an experiment, samples being siphoned from beneath a deep layer of paraffin oil from time to time for analysis. In this method the same criticisms apply as in the first case.

3. The maintenance of a steady rate of fresh water flowing over the fishes during the experiment, collecting samples from time to time and comparing with control samples. The apparatus used was somewhat modified from a setup employed by Keys ('30) in his studies on fish respiration, which it resembled in essentials. In this type of experiment the possibility of contamination by excretory products is at a minimum, but even here there is a chance for some effect from such a substance as carbon dioxide. The rate of flow must be slow enough to measure the amount of oxygen removed by the isolated fishes, and at the same time fast enough to maintain a supply of fresh water to the respiratory chambers, so that the diminished oxygen will not enter as a possible factor. The chambers used held 650 cc. and water passed through at rates varying from 1225 cc. per hour to 1425 cc. per hour.

It is very difficult to analyze with exactness the mass physiology of animals. The relationships which exist between volume of medium, the available space per organism, the effects of various environmental factors (oxygen concentration, excretory products, etc.) are so intricate that usually more than one variable is introduced. In this study eight fishes were used for every experiment. Four of these were grouped into one respiration chamber, and the other four separated into different chambers under conditions as identical with the group as possible. It is recognized that in this system the group occupies the same amount of medium as a single fish, but if space is allowed in proportion to numbers, then one element of crowding or aggregation is lost. In this study, then, unless otherwise specifically stated, a group of four fishes is compared with four isolated individuals and all the containers are treated as much alike as possible. Adequate controls were maintained in each case.

In most of the work on fish respiration the fishes are weighed and the oxygen concentration determined, after which some relation is established between the number of grams of fish and the amount of oxygen removed from the water. In the present work, however, because of the number of fishes used, it was judged better to measure the length of the fishes used and to use the same length throughout. Accordingly, for example, goldfishes with a similar history which measured from 4.00 to 4.20 cm. from the tip of the nose

to the base of the tail were selected for use. The mean length in centimeters was 4.10 with a standard error of ± 0.025 . As a check on the variability of this length of fish as to weight, ten goldfishes were weighed. The mean weight in grams was 1.800 with a standard error of ± 0.065 .

RESULTS

This work was started by testing an apparent discrepancy between the observed and expected ratios of oxygen consumption of isolated and grouped mudminnows. Four fishes were placed in an Erlenmeyer flask having a capacity of 1150 cc. and after the bottle was filled with water, stoppered, care being taken that no bubbles remained, it was allowed to stand for two hours and the amount of oxygen determined. The oxygen consumption of a group of four fishes was compared to that of four isolated fishes treated in a similar manner. Adequate controls were run in each case. All things being equal it is logical to expect that the group of four will consume approximately four times the amount of oxygen that a single fish uses, or approximately the same as that used by four comparable, but isolated, fishes. A consistent difference, however, soon led to the conclusion that some factor was modifying the oxygen consumption of the group (assuming that the consumption of an isolated individual is normal). The results of twelve experiments are shown in table I.

TABLE I. *Total amount of oxygen consumed by four isolated and four grouped mudminnows over a period of two hours. The temperature was practically constant (25°-26°)*

Control O ₂ tension at end of experiment in cc. per liter	Grouped		Isolated		Differ- ence in cc.
	O ₂ tension at end of experiment in cc. per liter	O ₂ con- sumed in cc.	Mean O ₂ tension at end of experiment in cc. per liter	O ₂ con- sumed in cc.	
6.49	6.02	0.54	6.25	1.10	0.56
6.39	6.04	0.40	6.06	1.52	1.12
6.69	5.97	0.83	6.21	2.20	1.37
6.26	5.80	0.53	6.00	1.20	0.67
6.56	6.08	0.55	6.40	0.74	0.19
6.45	5.95	0.57	6.34	0.51	-0.06
6.52	6.10	0.48	6.27	1.15	0.67
6.39	5.65	0.85	6.21	0.83	-0.02
6.55	6.05	0.57	6.31	1.10	0.53
6.37	5.92	0.52	6.22	0.69	0.17
6.53	5.62	1.05	6.26	1.24	0.19
6.65	5.96	0.79	6.37	1.29	0.50
Mean	6.49 $\pm$ 0.03	0.64 $\pm$ 0.05	6.24 $\pm$ 0.03	1.13 $\pm$ 0.12	0.49 $\pm$ 0.12

The figures in the columns of oxygen consumed refer to the total consumption of oxygen. This can be measured directly for the grouped fishes. For the isolated fishes it is necessary to summate the oxygen consumption of four different fishes to obtain the value. In both columns the values have

been corrected to account for the actual size of the container, so that the figure in each case represents the actual amount of oxygen consumed. These data indicate that at no time did the oxygen tension of the medium become lower than 5.62 cc. per liter for the group and 6.00 cc. per liter for the isolated fishes. Certainly at these tensions the decreased oxygen supply could not have been responsible for the lower oxygen consumption per fish for the group. The mean oxygen consumption for the four isolated fishes was 1.08 cc. while for the four in the group it was 0.64 cc. Considered statistically according to the method of Student ('25) these data have a value of 0.004, a figure which is well above the threshold of significance. Only two cases gave evidence that the total oxygen consumption of the isolated fishes was less than that of the group, and these were so small in comparison to the greater differences in the other direction that they have little effect on the general trend.

Experiments of this kind were repeated, using the guppy, and essentially similar results noted. The guppies, because of their smaller size (3.00-3.20 cm.) necessitated a longer time in the medium, and as a consequence, the experiments were allowed to run twelve hours. Table II outlines the results

TABLE II. *Effect of numbers present upon the oxygen consumption of the guppy. This experiment was conducted in a manner similar to those summarized in table I, except that a period of twelve hours was used. Temperature 20° C.*

Fishes	O ₂ present at end of experi- ment in cc.	O ₂ con- sumed in cc.	O ₂ consumed per fish in cc.
4	5.19	1.48	0.37
I	5.67	1.00	
I	5.70	0.97	0.96
I	5.75	0.92	
I	5.72	0.95	
0	6.67	—	

of one experiment of this type, and table III shows the summary of twenty-nine such experiments.

From table II it can be seen that instead of amounting to about four times the consumption of an isolated fish, under these conditions the group consumption was hardly more than that of a single individual. Table III shows the consistency of the results over a large number of experiments. At no time did the oxygen content of the medium become so low as to be a limiting factor. The lowest value of oxygen concentration in the grouped fishes was 2.30 cc. per liter, which is far above the asphyxial level, and in the isolated fishes the lowest oxygen concentration was found to be 3.84 cc. per liter. At these levels it is safe to assume that oxygen tension does not interfere with respiration. The significance, determined by Student's method, was found to be 0.0000.

The type of work in which the samples are taken at intervals during an

TABLE III. *Summarizing the results of twenty-nine experiments on the guppy. The procedure in the individual experiments was similar to that outlined under table I. Temperature 20° C.*

O ₂ tension at end in cc.	Average O ₂ consumption of a group of 4 fishes in cc.	O ₂ tension at end in cc.	Average O ₂ consumption of 4 fishes isolated in cc.	Differ- ence
5.12	0.39	5.52	0.99	0.60
3.39	0.54	4.68	0.71	0.17
5.19	0.37	5.67	0.96	0.59
5.23	0.36	5.52	0.92	0.56
4.73	0.29	5.44	0.44	0.15
5.53	0.12	5.31	0.32	0.20
4.85	0.27	5.46	0.46	0.19
4.82	0.28	5.37	0.41	0.13
5.46	0.09	5.53	0.36	0.27
5.42	0.14	5.58	0.27	0.13
5.17	0.21	5.59	0.37	0.16
5.38	0.23	5.81	0.35	0.12
5.20	0.27	5.73	0.40	0.13
5.31	0.25	5.71	0.49	0.24
4.43	0.29	4.68	0.72	0.43
4.89	0.26	5.33	0.47	0.21
5.24	0.17	5.45	0.34	0.17
4.60	0.52	5.99	0.48	-0.04
4.08	0.24	4.95	0.64	0.40
2.30	0.76	3.94	1.05	0.29
4.70	0.33	5.24	0.44	0.11
4.75	0.21	4.86	0.54	0.33
4.89	0.22	5.00	0.66	0.44
3.29	0.34	3.84	0.60	0.26
5.24	0.14	5.11	0.33	0.19
2.92	0.59	4.32	0.63	0.04
5.13	0.35	5.80	0.43	0.08
5.22	0.14	5.34	0.44	0.30
4.85	0.27	5.46	0.46	0.19
Mean 4.74±.14	.30±.01	5.25±.10	0.54±.04	.24±.03

experiment is illustrated by the work on the common goldfish, a hardy form, and one much used in laboratory work.* A group of four fishes was placed in an Erlenmeyer flask, and was covered with three or four centimeters of a heavy paraffin oil, which was found to be quite effective in isolating the medium from the atmosphere, at least in the interval used. The group of four fishes was compared from time to time with four isolated fishes under similar circumstances. An oil covered blank was run simultaneously in order to check on the original concentration, and on the effectiveness of the oil in maintaining a block.

As stated above, this method also allows an opportunity for the action of carbon dioxide and other products of metabolism that may accumulate as the time progresses, and for a gradual decrease in the oxygen concentration of the medium. Experiments of this type are of value, however, because the comparison of groups and isolated individuals has been the major point of interest, and any effect of crowding will only serve to bring out more effectively the difference which exists between fishes under these different conditions.

Twelve experiments were performed, ten with the volume of 2175 cc. and two with the volume of 1150 cc. In both of these cases the same principles are illustrated, the only difference appears to be a somewhat quicker diminution of the oxygen supply in the smaller volume. Table IV and figure 1 show the results of ten experiments with goldfishes in the two liter volumes. In figure 1 the average oxygen consumption per fish from the beginning of the experiment is shown in hourly intervals over a period of nine hours. It is

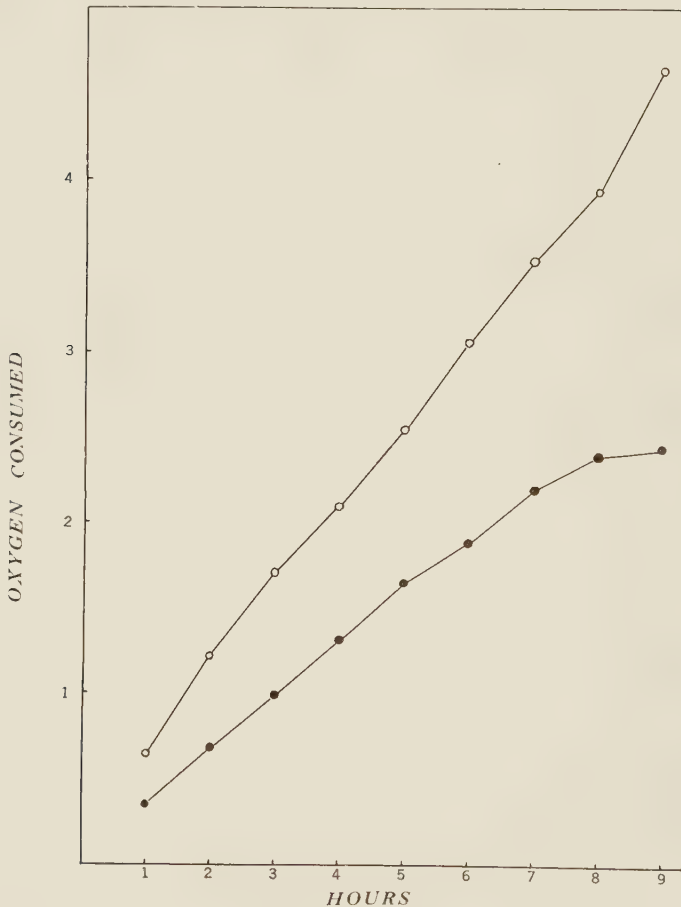


FIG. 1. Difference between grouped and isolated fishes over a period of nine hours. These results are in cc. oxygen consumed. $\circ$ = isolated. $\bullet$ = grouped.

apparent that fish for fish the amount of oxygen consumed is much less in the members of the group than in the isolated individuals. The significance in all cases is far above the threshold as determined by Student's method.

An examination of the curves in figure 1 will also reveal that the rates of oxygen consumption appear to be quite constant. The only exception to this

TABLE IV. *Mean total amount of oxygen consumed in cc. hour by hour by grouped and isolated goldfishes. This table is based upon ten experiments. Standard errors are shown. Temperature 26°-27° C.*

Hour	Group of 4 fishes	4 Isolated fishes
1	0.362±0.029	0.642±0.032
2	0.686±0.045	1.225±0.053
3	0.996±0.051	1.705±0.066
4	1.311±0.070	2.112±0.107
5	1.647±0.077	2.551±0.153
6	1.881±0.079	3.038±0.150
7	2.209±0.052	3.564±0.163
8	2.405±0.047	3.945±0.154
9	2.450±0.011	4.660±0.095

seems to be the termination of the group curve, which flattens out perceptibly after the seventh hour. Up to this time, however, there is no particular irregularity in the rate of oxygen consumption. Under these experimental conditions it is admitted that excretory products are accumulating, and that the oxygen supply is constantly being reduced. If such a product as carbon dioxide, however, is responsible for this phenomenon, then its effect should be shown before the seventh hour, since it is being produced from the beginning of the experiment. The constancy of oxygen consumption during most of the experiment indicates that the changes produced by the fish or fishes living in this restricted experimental volume which includes the accumulation of carbon dioxide and the decreased oxygen are not limiting factors during the early hours of the experiment.

Figure 2 is designed to show the relation between the total consumption of oxygen in groups and isolated individuals and the oxygen tension of the medium. As mentioned above, the respective rates of consumption are quite constant down to near the level of asphyxia, where the consumption is reduced near the seventh hour. Thereafter the consumption difference between the grouped and isolated fishes grows progressively larger on account of the decreased rate of consumption by the grouped fishes. Such differences are without question of significance.

A somewhat more convincing type of experiment is shown in fig. 3 where the groups and isolated fishes were alternated. The isolated fishes of one experiment were placed together and used as the grouped fishes of the next. The group, on the other hand, was separated and the members used as isolated fishes. Unfortunately, this was possible in only three cases, since the post-experimental mortality of the group in these long experiments often amounted to as much as fifty per cent of the individuals. In many of the experiments one or more of the grouped fishes would succumb to the effects of the treatment, and in these cases the fishes were removed as soon as their death was ascertained, and the entire experiment terminated at the following hour. Figure 3 indicates that the fishes consume oxygen at a rate that is strongly influenced, and in fact apparently controlled by the number of individuals present.

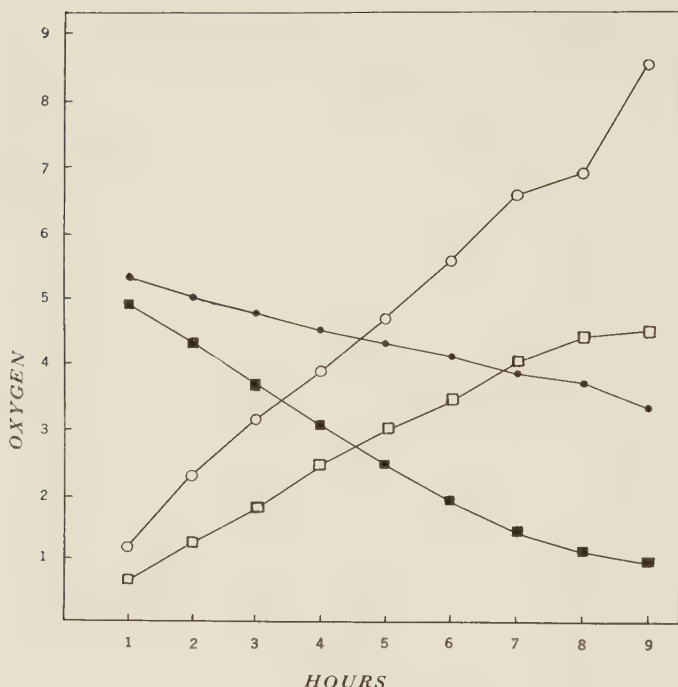


FIG. 2. Relation between the total oxygen consumption in groups and isolated individuals and the oxygen concentration of the medium. ● = Average O_2 tension in cc. per liter of medium of isolated fish. ■ = Average O_2 tension in cc. per liter of medium of grouped fishes. ○ = Average total consumption of four isolated fishes in cc. □ = Average total consumption of four grouped fishes in cc.

The work of Keys ('30) on the respiration of fishes has shown that the best way of measuring the oxygen consumption is to keep running water flowing through the respiratory chambers, thus supplying the fishes with a fresh oxygen supply, and at the same time minimizing the chances for a contamination by excretory products.

An arrangement, similar in principle to that of Keys, was employed and the results obtained as to the relative oxygen consumption of groups and isolated fishes in eight experiments with running water are shown in fig. 4.

The source of water was a large carboy in which Whitman Laboratory well water was aerated and from which it was siphoned to the respiratory chambers. These chambers had a capacity of 650 cc. and the rate of flow was controlled by limiting the outgo by capillary tubes. All chambers were supplied from a common source. The capillary tubes varied somewhat and it was necessary to measure the rate of flow through each one separately. It was found that the rates varied from 1225 cc. per hour to 1425 cc. per hour. Five chambers were run simultaneously, one containing a group of four fishes, and the other four containing one fish each. The entire apparatus was

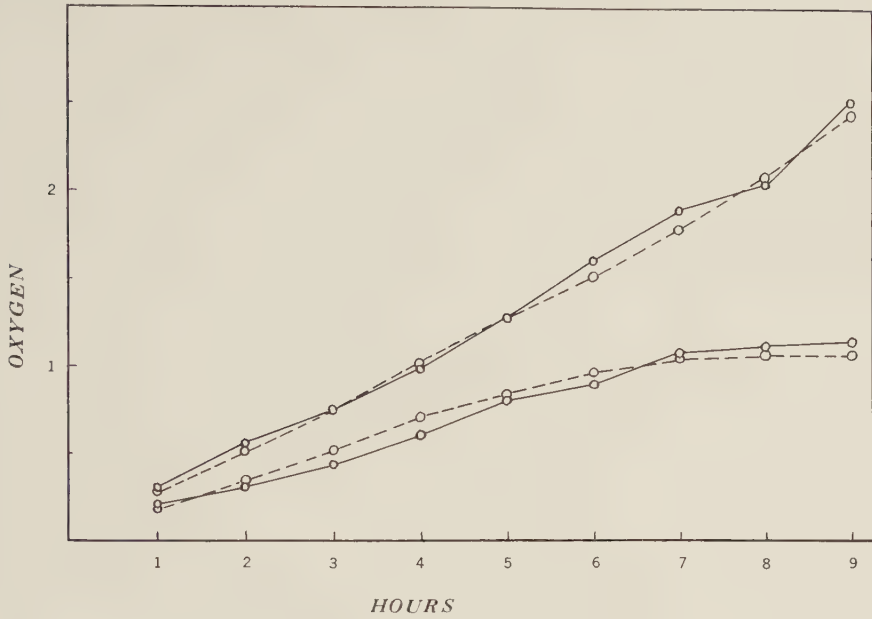


FIG. 3. Results of three experiments in which the isolated and grouped fishes were reversed. Solid lines show the condition before reversal, the upper line representing the consumption of the isolated fishes, the lower line that of the grouped fishes. Dotted lines show the condition after reversal, the upper line representing the isolated fishes and the lower line the grouped fishes.

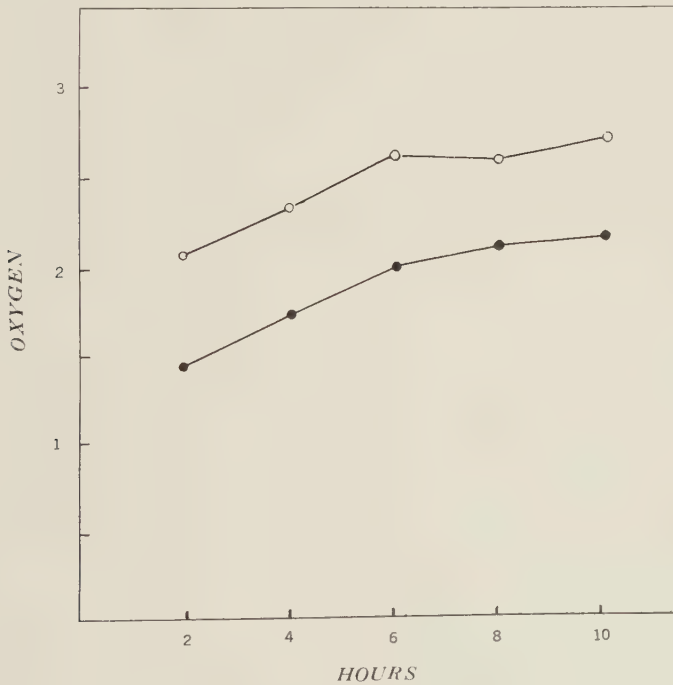


FIG. 4. Difference between grouped and isolated fishes in running water.
● = Group. ○ = Isolated.

immersed in a water bath, and the temperature controlled to any desired point. Samples were drawn from the capillary tubes for analysis. As a check on the oxygen tension of the supply water, samples were drawn from the main siphon line before it reached the respiratory chambers and analyses made. Knowing the oxygen tension before and after the water had passed through the chambers, and knowing the rate of flow, it was possible to calculate the amount consumed by the fishes. At all times the consumption of oxygen in the group was less than the consumption of the isolated fishes. Table V also

TABLE V. *Difference in oxygen consumption at two hour intervals between four grouped and four isolated goldfishes in running water experiments. Data represent average of eight experiments. Temperature 22° C.*

Hour	Mean O ₂ consumed in cc.		Significance of difference ³
	Group of 4	Isolated	
2	1.44 ± 0.06	2.02 ± 0.11	0.0000
4	1.73 ± 0.13	2.31 ± 0.16	0.0024
6	1.95 ± 0.16	2.66 ± 0.26	0.0040
8	2.07 ± 0.16	2.60 ± 0.25	0.0068
10	2.16 ± 0.34	2.85 ± 0.41	0.0034

³ 0.01 or less is usually regarded as having statistical significance.

shows the mean oxygen consumed during these flowing water experiments in cc. per liter, and the significance at two hour intervals over a period of ten hours.

Experiments of this nature were performed upon the Atlantic killifish and similar results noted. The fishes selected were all of the same size and were supplied with flowing sea-water at all times. A measurement of the oxygen tension of the water before and after use by the fishes made it possible to calculate the amount of oxygen removed by the fishes. Table VI shows the

TABLE VI. *Amount of oxygen consumed per fish by grouped and isolated Fundulus under identical conditions. Results in cc. per fish. Temperature 22° C.*

Group of four	Isolated	Difference
0.525	0.822	0.297
0.610	0.877	0.267
0.415	0.747	0.332
0.455	0.781	0.326
0.310	0.816	0.506
0.670	1.167	0.497
0.632	0.738	0.106
0.475	0.886	0.411
Mean 0.512 ± 0.040	0.854 ± 0.045	0.343 ± 0.036

oxygen consumed per fish by grouped and isolated animals in eight experiments.

Each of these experiments was performed on a different day, so that the variation which exists between different experiments is not necessarily significant. The conditions under which each individual experiment was run,

however, were as constant as possible. The significance of this group of data when tested by Student's method was found to be 0.00007, which is far above the threshold.

Experiments on *Fundulus* also afforded an interesting example of the reversible nature of the "group effect." The oxygen consumption of the fishes was followed over a period of several days, during which time individual fishes were used as isolated forms, as members of a group of two, and as members of a group of four. The amount of oxygen consumed can best

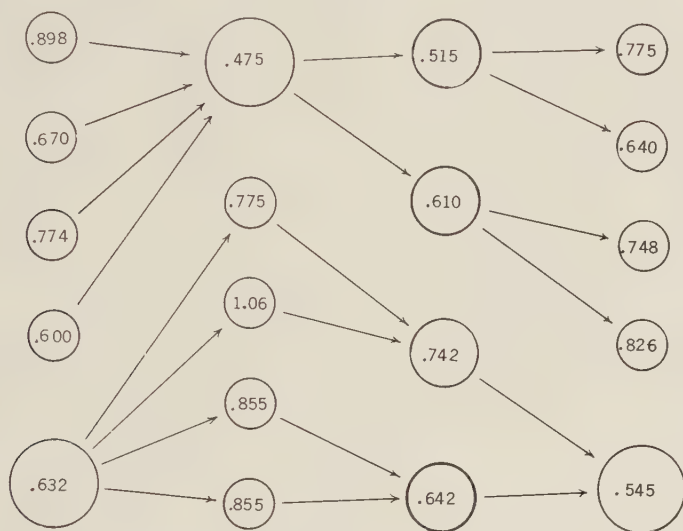


FIG. 5. Change in oxygen consumption of *Fundulus* according to the number of fishes present. The size of the group is indicated by the size of the circle. Groups of one, two, and four were used, and fishes alternated between these groups. Each column indicates a day. The numbers represent the amount of oxygen consumed in cc. per fish.

be seen by means of figure 5. Thus, it appears that the oxygen consumption of any one fish depends, in part at least, upon the number of individuals present in the respiratory chamber.

The data so far have indicated that a group effect is present when the volume is held constant. By putting fishes into volumes in proportion to the numbers present, however, one element of crowding is lost, and the situation becomes less complex. Such a series of experiments was conducted, and the results shown in table VII. In these experiments a group of four goldfishes was placed in an Erlenmeyer flask which contained two liters of water under the usual thick layer of paraffin oil, and four isolated fishes of the same size were distributed to four half liter flasks in exactly 500 cc. of water under a similar oil layer. Controls were run as before. The data indicate that volume plays a part in controlling the oxygen consumption of the fishes. The "group effect" is lost, and the average consumption of the grouped and

isolated fishes is practically equal. By Student's method the significance was found to be 0.2972 which indicates that the difference between the oxygen consumption of the grouped and isolated fishes, although still greater for the latter, is in this case far from being statistically significant.

TABLE VII. *Amount of oxygen consumed in one hour by grouped and isolated goldfishes when the volume of medium is in proportion to the number of individuals present. Temperature 24° C.*

Grouped		Isolated	
O ₂ tension at end in cc.	O ₂ con- sumed in cc.	O ₂ tension at end in cc.	O ₂ con- sumed in cc.
5.56	0.76	5.46	0.61
6.96	1.28	6.86	1.35
5.78	1.48	5.71	1.83
5.69	0.64	5.47	1.61
5.34	1.36	5.52	1.19
5.13	1.12	5.05	1.09
4.80	1.28	4.86	1.10
4.55	1.26	4.73	1.06
4.52	0.96	4.59	1.08
4.39	0.08	4.05	1.14
4.97	1.06	4.79	1.31
Mean 5.24 ± .22	1.03 ± .11	5.19 ± .22	1.22 ± .09

DISCUSSION

Some animals appear to consume oxygen at a rate proportional to the concentration of this gas in their medium, while others are largely independent of the oxygen concentration of the surrounding medium, at least until quite low levels are reached. This whole question has been reviewed at some length by Hyman ('29) so that it seems inadvisable to make a repetition here. An important paper, however, that deserves attention is that of Toryu ('27), which lends considerable weight to the view that fishes are quite independent of the medium tension until the pressure is reduced to the region of 0.2 (vol. per cent), where the consumption begins to fall off. Between 0.2 and 0.75, however, the rate of consumption is very constant. More recently, Keys ('30) on fishes, and Hiestand ('31) on several invertebrates bring the problem up to date with important criticisms of previous work and the applications of more refined methods to the study of respiration. The work of this paper, although not its primary concern, shows that within considerable ranges the oxygen consumption is independent of the oxygen tension of the medium. At lower levels, however, the oxygen consumption falls off. This falling off took place under the conditions of these experiments when the level of oxygen tension was in the region of one cc. per liter.

The aggregational aspect of this question has received little attention in comparison to the great body of data that exists concerning general respiration. Allee ('26) has shown that the rate of oxygen consumption in two

genera of land isopods is less with bunched individuals than with isolated animals at the beginning of the experiments. At the end of twenty-four hours, however, this relationship is reversed, and the scattered isopods are consuming oxygen at a slower rate than are the bunched individuals. A similar phenomenon has been shown for the serpent-star, *Ophioderma* (Allee, '27). The grouped forms at the beginning of a starvation period consumed less oxygen than did isolated individuals, but later this relation is reversed, as in the isopods, and the individual serpent-stars had the slower rate of oxygen consumption.

With the fresh water isopod, *Asellus* (Allee, '29) it has been demonstrated that individuals taken from an aggregation in nature consume oxygen at a slower rate than do isopods selected from scattered individuals.

Fowler ('31) shows that significant differences exist between the oxygen consumption of grouped *Daphnia* and that of isolated individuals. The data presented by Fowler appear to show a condition very similar to that of the fishes.

These studies are the only ones known which treat with respiratory differences in grouped and isolated individuals. In the applicable cases cited it was found that during the earlier stages of the experiments grouping was accompanied by a reduction in oxygen consumption. The data presented in this paper show that this is true in certain fishes for at least ten hours. These data appear to be comparable with the first stages of Allee's experiments. They were not continued long enough, and except for the running water experiments, they were not run under the proper conditions to test whether or not a reversal such as he describes would result. Such possibilities remain to be worked out.

It is difficult to account for the difference between group respiration and that of isolated individuals. A number of things at once suggest themselves as possible factors for producing this effect. The factor of reduced oxygen content is the most obvious possibility. This, however, can hardly be said to be of importance since these experiments confirm Toryu's ('27) findings that the oxygen consumption of fishes is quite independent of the oxygen concentration of the medium down to near the asphyxial level. The "group effect" was found to be present at all times: Again, the experiments with running water, in which the oxygen content never approached the asphyxial level, the "group effect" was still prominent. With these facts in mind oxygen tension cannot be regarded as of primary importance.

Excretory products, such as carbon dioxide, may be thought of as having a part in the lowering of the oxygen consumption of the group. Carbon dioxide is produced at all times by the fishes, so that its concentration in the medium grows progressively larger. In view of this it might be expected that the effect of carbon dioxide would reduce the oxygen consumption gradually. This was not found to be true. Well water was used in all the experiments, and the Whitman Laboratory well water is highly buffered with cal-

cium salts. Changes in pH could not be detected by colorimetric methods in the experiments run two hours, and yet the "group effect" is outstanding in these experiments. In the running water experiments, on a basis of the evidence at hand, the more rapid production of carbon dioxide by the grouped fishes cannot be used to account for differences between grouped and isolated fishes.

Activity of some kind might be thought of as a possible factor. Allee ('27), using serpent-stars, was dealing with positively thigmotactic animals, which tended to collect in bunches. The decreased oxygen consumption in the early stages of his experiments has been attributed in part, at least, to "a decreased muscular tonus accompanying the more nearly optimum tactile relations furnished by the bunched condition." With the fishes used in this work, however, there is no such tactile tropic response. The conditions imposed upon the fishes by the Erlenmeyer flasks are not as remote from their natural habitat as are the same conditions for serpent-stars. At least, no difference could be detected between the activity of groups and isolated individuals by the observational method, although no quantitative methods were employed in this determination.

Volume seems to play some part in controlling the oxygen consumption of fishes, since by allowing volume in proportion to the number of individuals present, the "group effect" is lost, and the amount of oxygen consumed by the fishes in the group and the isolated individuals is essentially the same. This fact, while interesting, helps little in explaining the "group effect" when the volume per group and per individual is the same.

Ecological investigations have for years been concerned with the detection and measurement of the effect produced by environment upon the organism. Much of the effort of the ecologist has been devoted to an analysis of the physical aspects of the environment, and to the relationships of individuals or communities to these physical surroundings. Biotic factors, on the other hand, have not, until comparatively recently, received the same attention. It is becoming increasingly clear, however, that delicate and subtle biotic mechanisms are at work within the confines of a restricted environment, and that these produce definite and important changes in the interactions within such a community. As stated in the introduction to the present report, many of these relationships have recently been reviewed by Allee ('31) who found that these biotic effects may be classified according to whether they produce beneficial or harmful results. The biotic effects reported in this paper are not easily incorporated into such a scheme. Whether reduced oxygen consumption among members of a group is harmful or beneficial for the individual depends on the other conditions that are operating. It is evident, however, that the behavior of the individuals of a group is modified in response to the presence of others, and that the modification can be measured by differences in oxygen consumption under conditions when more obvious behavior effects cannot be observed. Such facts must be considered in ecological studies on

community organization. The effects noted here have been found in relatively simple communities, but until otherwise demonstrated, it is logical to assume that such effects are also present in the more complex communities in nature.

CONCLUSIONS

1. When four fishes are present in a given volume the amount of oxygen consumed per fish is lower than the amount consumed by an isolated fish in the same volume.

2. This phenomenon has been observed in four genera of non-schooling fishes, and it is suggested that it may be a general rule for all such fishes.

3. The "group effect" is found to be reversible, and the respiration of any individual fish can be altered by increasing or decreasing the size of the group.

4. When the volume per fish is the same for grouped and isolated fishes the difference in oxygen consumption is not of statistical significance.

5. Reasons for the "group effect" are not clear at present, but such factors as accumulation of carbon dioxide or reduction of oxygen tension do not appear to be important, since this effect appeared before these became limiting factors. Investigations are now in progress to determine the nature of this phenomenon.

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